

Chapter 24

Ecophysiology, Biodiversity and Sustainable Management of Central Amazonian Floodplain Forests: A Synthesis

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Abstract This synthesis chapter provides an overview of the 23 chapters of this book. With more than 1000 tree species, Amazonian floodplain forests are the most diverse forests of this kind. They occur in different forms and under different hydrological and chemical (water and soil) conditions. Forests in nutrient rich whitewater river floodplains (várzeas) are richer in species, more dynamic, and more productive than those of black- and clearwater rivers. The new species colonization concept explains the relationship between upland and várzea forests. A model of forest succession is provided that indicates the development of different seral stages under different hydrological and sedimentological conditions. Trees react to long-term flooding and water-logging of the soils with many anatomical, morphological, physiological and phonological adaptations, which result in specific life history traits. Seed production, seedling establishment, and sapling survival are of fundamental importance for the regeneration of these forests and their reactions to the frequent set-backs caused by erosion and sedimentation processes. Until now, the use of floodplain forests has been restricted to highly selective timber exploitation, which depletes the stocks of the respective tree species. A management model, based on growth-oriented logging (GOL) is provided here. In this model, the extraction of the logs depends on water levels, the maximums and minimums of which can be predicted using new model based on sea surface water temperatures in the Pacific and the Atlantic Oceans. Such predictions would facilitate the management of the natural resources of the varzea, including management using forestry. When the many riparian forests are included, floodplain forests cover about one third of the Amazonian rain forest area. However, this fact has not been considered in management aspects and climate models for Amazonia. Global climate changes certainly will affect the hydrological cycle in Amazonia. However, we consider the prediction by the Hadley Center of a near “savannization” of the Amazon forest to be without sufficient scientific basis and unhelpful, because it may even accelerate the deforestation of Amazonia. The maintenance of intact wetlands will be very important for the sponge function of the landscape, which acts to retain water and to buffer extremely dry and wet periods. In this context, the floodplain forest is of utmost importance as a refuge for many plant and animal species.

24.1 Introduction

Amazonian floodplain forests have called the attention of scientists since the time of the expeditions of natural historians, because access to the central Amazon basin was possible only by the rivers and naturalists were impressed by the vast and deeply flooded forests. More detailed taxonomic studies started in Brazil at the end of the nineteenth century (Junk and Piedade 2010). Since the 1960s, many studies were performed on limnology, fish and fisheries, general use of the várzea, the natural history of floodplain forests, and socio-economic aspects of the riverine population. These studies have been summarized in several books and proceedings (Sioli 1984a; Ayres 1993; Goulding 1980; Goulding et al. 1996; Junk et al. 1997; Sternberg 1998; Smith 1999; Padoch et al. 1999; Junk et al. 2000a; and others). Detailed studies on biodiversity, primary production, ecophysiology and sustainable management started only a few decades ago. The results of these studies are presented in this book.

Aim of this synthesis chapter is to summarize the information provided in the individual chapters about central Amazon floodplain forests, to discuss the major findings in a comprehensive approach, to call attention to major gaps, to point to the economic potential of the sustainable management of the forests for the local population, and to discuss actual and future threats including impacts of future regional and global climate change.

24.2 Age and Evolution of Amazonian Floodplain Forests

The Amazon basin is a very old depression, which existed already in the Precambrian period on the Gondwana continent. When South America separated from Africa in the Early Cretaceous period, about 110 million years ago, the basin became closed in the West by the uprising Andes. The paleo-Amazon drained westward to a large depression which extended along the eastern side of the Early Andes and was connected in the North to the paleo-Caribbean Sea. In the following periods several marine transgressions occurred in the Late Cretaceous (83–67 Ma), the Early Tertiary (61–60 Ma), and the Late Tertiary (11.8–10 Ma) periods, as indicated by marine sediments. They alternated with periods in which freshwater swamps and lakes prevailed. Large freshwater lakes were formed in the Tertiary period (Lago Pozo in the Middle Eocene–Early Oligocene, 43–30 Ma; and Lago Pebas in the Late Tertiary, 20–11.8 Ma). They were filled with sediments of riverine origin from the Andes and the shields of Central Brazil and the Guianas. In the Late Miocene (8 Ma), the connection to the Caribbean Sea and the Orinoco basin was closed by the Vaupes Arch. The Amazon River opened its way to the Atlantic Ocean by breaching the Purus Arch, and the modern Amazon drainage system incised large valleys and floodplains in the soft sediments (Lundberg et al. 1998).

During the entire period, the area remained near the equator and we can assume a hot and humid climate. During periods of marine transgressions, freshwater habitats became separated from each other favoring speciation of aquatic and palustric organisms

by genetic separation. In periods of extended freshwater swamps and lakes, the species conquered large areas and new habitats until the next marine transgression separated the populations again. The large number of fruit-feeding and seed dispersing fishes (ichthyochory) point to the co-evolution of floodplain forests and fishes. Fossils indicate that over the course of the last 13.5 million years or longer, fish such as tambaqui (*Colossoma macropomum*), which apparently has not changed its diet of fruits and seeds (Lundberg et al. 1998; Lundberg et al. 1998), have persisted.

During Quaternary times periodic oscillations in global climate led to alternating glacial and interglacial periods which resulted in changes in the water level of the oceans worldwide (Irion et al. 2010). These changes affected the lower course of the Amazon River by increasing the slope during marine low water periods (Irion et al. 2010). Dramatic hydrologic changes started approximately 900,000 to 600,000 years ago during the so-called Mid Pleistocene Revolution (Berger and Wefer 1992). From this time on sea level changes reached 100 m and more, and affected the floodplains along the lower courses of all large Amazonian rivers until 3,500 km inside the continent. During marine low water periods, the rivers excavated deep valleys, which they filled up with sediments during the following interglacial high sea levels. Parts of the old sediments remained and form the Pleistocene várzeas. These areas can be found at the today's high water level or they reach up to 20 m or more above it. The height of some Pleistocene várzeas in western Amazonia is in part explained also by a slow raise of the area by tectonic activity. The fluvial origin of the Pleistocene várzeas can be shown by geomorphologic features characteristic for river floodplains, such as ridges and swales, but also by mineralogical and chemical composition of the sediments, which show much larger similarity to the recent river sediments than to the surrounding tertiary soils (Irion et al. 2010).

During the last glacial period, the sea level was about 130 m lower and the slope of the Amazon river several times larger than today. This had a dramatic impact on the hydraulic geometry of the Amazon River and its large tributaries. There is a controversial discussion about the paleo climate in Amazonia during the last glacial period. Several authors postulate a dryer and cooler climate and the retreat of the Amazon rain forest to a few forested areas interspersed in savannah vegetation (refuge theory) summarized by Haffer and Prance (2001). Other authors reject this theory, summarized in Colinvaux et al. (2001). Studies of Irion et al. (2010) on a 50 m sediment core of the mouth bay of the Tapajós River also do not support this assumption. Considering an increased slope of 130 m to the Atlantic Ocean and a similar discharge than today, we postulate that the Amazon River changed its behavior from interglacial meandering to glacial braiding with high current velocity and strong erosive forces. At that time, the floodplain surface of the Amazon River near Manaus was about 40 m lower (Irion et al. 2010). Fluvial-morphologic units were subjected to a much higher dynamic than today and probably had turnover periods of a few decades to centuries in comparison to today's turnover periods of centuries to millennia. We assume that therefore much larger areas were covered by pioneer forests or early successional stages than today, but there were certainly sufficiently large areas available with turnover periods of several centuries to allow the development of mature floodplain forests dominated by the respective set of species. Today's large number of flood adapted trees point to low extinction rates during long geologic periods.

24.3 Extension, Distribution and Classification of Wetland Forests

Estimates about the extent of wetlands in Amazonia vary considerably. The highest number was given by Klinge et al. (1990) and Junk (1993) who related about 1 million square kilometers to large river floodplains and large interfluvial wetlands and another one million square kilometers to narrow stripes of riparian wetlands along streams and low order rivers. The first number has now been confirmed by the analysis of remote sensing data (Melack and Hess 2010). Extended wetlands occur in the upper Madeira River, the Negro River, the Araguaia River, and along the Amazon River and its white-water tributaries Purús, Juruá and Japurá. According to these authors, about 80% of the flooded area is covered by flood tolerant forest and shrubland. Our studies show that most of the wetlands along low order rivers are covered by riparian forest. If Junk's estimate of 1 million square kilometers of riparian wetlands holds true, the total area of forest subjected to periodic water logging or long term flooding increases to about 1.8 million square kilometers, corresponding to one fourth of the Amazon basin and 35% of the central Amazonian rain forest area of about 4.6 million square kilometres. The remaining 200,000 square kilometres belong to riparian forests in the *cerrado* belts. This estimate changes dramatically the view on the Amazon rain forest, which has been described largely as non flooded, *terra firme* forest. Flooding or water logging of the soil has to be considered an environmental factor that affects about 30% of the forests in the Amazon basin, with far reaching consequences for the physiology of the trees and edaphic processes, which affect the entire biome including the atmosphere. This aspect has been neglected so far in ecological studies concerning the role of the Amazon rain forest in the global climate change debate, as well as the impact of regional climate change scenarios on Amazonian wetlands and their vegetation.

Amazonian wetlands occur in great heterogeneity. A classification system is still missing, but urgently needed (1) for a better comparability of the results of wetland studies, (2) for the elaboration of research projects to close major gaps in wetland research, and (3) for the establishment of a national wetland policy to sustainably manage and protect wetlands and their resources, including biodiversity. First attempts to elaborate such a classification are ongoing in the State of Amazonas (Junk and Piedade 2005) and the Pantanal (Nunes da Cunha and Junk, in press). These classification efforts base on hydrological, water- and soil-chemical, and botanical parameters, as did Prance (1979), who elaborated the first classification system for Amazonian wetland forests. We consider this approach very useful and have adopted it with minor modifications (Junk and Piedade 2010; Table 24.1).

As Wittmann et al. (2010) have shown, species composition in floodplain forests varies considerably according to the position on the flooding gradient but also along the river axes and between river basins. Therefore the major classification units in Table 24.1 will be subdivided in future in different subunits according to species composition, as soon as enough regional data are available.

Table 24.1 Key to the principle types of Amazonian forests subject to inundation, according to Prance (1979), modified

Periodically inundated forests	
Flooded by regular annual cycles of rivers	
White-water	1. Seasonal várzea
Black-water and clear-water	2. Seasonal igapó
Flooded by tidal movements	
Saltwater	3. Mangrove
Freshwater backup	4. Tidal várzea
Flooded by irregular rainfall (flash floods)	5. Riparian forests along low-order rivers ^a
Long-term inundated forests^a	
White-water	6. Várzea swamp forest, várzea chavascal ^a
Black-water and clear-water	7. Igapó swamp forest, igapó chavascal ^a

^aOur modifications

24.4 Evolution, Species Diversity and the Tree Species Colonization Concept

24.4.1 Tree Species Diversity

Despite consisting of partially highly adapted and many endemic tree species, Amazonian floodplain forests are the most-species rich floodplain forests world-wide (Wittmann et al. 2010). The importance of increased habitat diversity and isolation of subpopulations by river dynamics for speciation has already be pointed out by Salo et al. (1986) for sub-Andean western Amazonia where geologic activity and river dynamics are much higher than in central Amazonia. Flooding and the hydro-ecologic connectivity of the vast Amazonian river system allow for ecological processes and predictable aggregations of tree species over huge geographic distances. Nonetheless, with an increasing species diversity from eastern to western Amazonia, tree species diversity variations and oligarchies in Amazonian floodplains seem to follow environmental gradients and rules similar to those of Amazonian terra firme. This demonstrates the existence of intense ecological interactions and species migrations between both ecosystems (Wittmann et al. 2010).

Low-várzea forests are richer in endemic tree species than high-várzea forests, where continuous species migrations between flooded areas and the non-flooded uplands are most probable to occur (Wittmann et al. 2010). Together with the evidence that high-várzea forests are floristically more similar to the uplands than low-várzea forests Wittmann et al. (2010) proposed a Tree Species Colonization Concept for Amazonian floodplain forests (Fig. 24.1).

The concept implies that flooding and the associated hydro-geomorphologic dynamism of the Amazonian rivers act as a natural regime of disturbance on tree species establishment and distribution, thus providing extreme environmental

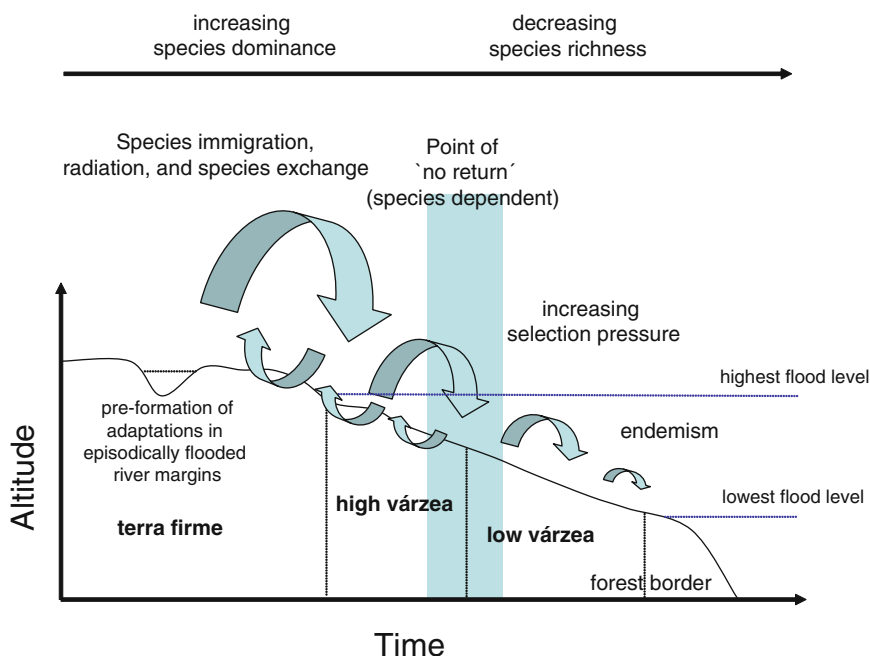


Fig. 24.1 Species Colonization Concept in várzea floodplains

conditions, which directly influence on speciation processes throughout the Amazon basin without requiring geographic or tectonic barriers. Therefore, periodic floods combined with the related hydro-geomorphologic dynamism of the rivers maybe one of the most important environmental triggers for speciation (Ferreira et al. 2010; Wittmann et al. 2010), and thus one of the main reasons for the exceptional high tree species diversity within the Amazon basin. There are some evidences that large part of recent equatorial upland forests were influenced by floods during one or several periods of landscape evolution, especially during Pleistocene and Holocene warm periods, when the sea-level was comparatively high (Irion et al. 2010). On the other hand, constantly migrating river-channels especially of the Amazonian white-water rivers affected large part of western equatorial Amazonia, and defined physical and chemical soil characteristics also within the substrates of recent uplands. Studying the flora of recent upland and floodplain forests thus provides data and evidences about landscape evolution, and allows for the creation of speciation and species distribution models in both the past and under future climate change. In this context, our knowledge about species migrations and the ecological interactions at the aquatic terrestrial transition zone (ATTZ; Junk et al. 1989) is extremely scarce. More comparative floristic inventories in both floodplain and terra firme forests are needed to fulfill this gap of knowledge in order to allow for reliable interpretations of the evolution of the Amazonian flora.

24.4.2 Floodplain Forests as Habitats for Associated Animal Species

The Amazonian floodplain forests provide important habitats for a large variety of animals. Best studied are the importance of the forests as food source for the fishes and the dispersal mechanisms of seeds (ichthyochory) (Parolin et al. 2010b; Goulding 1980). Large scale forest destruction will severely affect local fishery, because many commercially important fish species rely on fruit and seeds from the forest. Two monkey species, the White Uakari (*Cacajao calvus calvus*) and *Saimiri vanzolini* are endemic to the várzea forests. In a study on birds of the Marchantaria Island in the Amazon near Manaus, Petermann (1997) registered about 210 species. Some of them are restricted to forest patches, many using scrub communities on lake sides and sand bars. Many wading birds use trees for resting at night and nesting. Petermann attributes the low number of forest bird species at Marchantaria island to the patchy distribution of forested areas, strong human disturbance and isolation of the island in the middle of the main channel of the Amazon River. This points to the importance of large, undisturbed forest areas for bird species diversity in Amazonian floodplains (Queiroz and Peralta 2010).

Of specific importance is the floodplain forest for species diversity of terrestrial invertebrates. Adis (1997) differentiates between terricolous and arboricolous species. Arboricolous species live mostly on the tree trunks or in the canopy. But many terricolous species also use the trees to escape flooding during the high water period. Periodic flooding reduces invertebrate species numbers in Amazonian floodplains in comparison to non-flooded habitats, but creates many specific survival strategies and endemic species.

An analysis of beetle communities in the canopies of different forest types confirms lower species diversity in the floodplains in comparison to terra firme forests but high site specific variability between different floodplain forest types. The authors relate these findings to greater tree species diversity in the terra firme, differences in tree species composition in the floodplain forests, and flood stress (Adis et al. 2010). The authors postulate that local deforestation will result in the loss of many unique restricted beetle species. This statement holds certainly true for terrestrial invertebrates in general.

24.5 Community Structure and Succession

Species distribution, diversity, and forest succession in Amazonian várzea forests is partially well-described. Abiotic variables, such as flood height and duration, sedimentation rates, distance from the main-river channels, soil texture, and solar radiation on the forest floor, but also biotic variables, including species richness, stand density, stand architecture, mean wood density, and increment and growth rates of trees, are variables that change during forest succession and interact with each other. Therefore, many várzea tree species can easily be classified as pioneer,

secondary, or late-successional species, and the rules of forest succession allow for a certain predictability of forest type establishment and species diversity (Wittmann et al. 2010; Fig. 24.2).

However, the alluvial dynamism continuously changes in spatial and temporal scales. The time scale for the development of the different várzea forest types range from a few years in pioneer stages near the highly dynamic river banks to several centuries or even millennia in low-dynamic backwater depressions and high-várzea forests. Combined with continuous channel migrations of the white-water rivers, the alluvial landscape is characterized by a small-scale mosaic of different forest types. This complicates the rapid assessment of tree species richness in várzea forests at larger scales, and often implies the need for very detailed floristic inventories to secure an adequate and sustainable management of the várzea landscape.

There is, on the other hand, a gap of knowledge about species composition and diversity, forest structure, and succession in Amazonian igapó. The existing data suggest that igapó forests are characterized by a distinct flora that shows low floristic similarities to other Amazonian ecosystems, including the várzea (Wittmann et al. 2010). Due to the generally low sediment load of Amazonian blackwater rivers, igapó forests are characterized by the long-term stability of periodically flooded habitats. Combined with the paucity of nutrients, forest succession in Amazonian igapó occurs in longer time-scales than in Amazonian várzea, and trees are characterized by reduced growth rates (Schöngart et al. 2010), which possibly induce higher maximum tree ages than those reported for várzea trees (Schöngart et al. 2005). This directly influences the community structure of Amazonian igapó forests, and is an important trait for the management of forest resources. There is an urgent need for floristic inventories and ecological studies in Amazonian igapó, in order to create the basic knowledge about species composition, diversity variations, and tree growth behaviour in dependence of the abiotic environment.

24.6 Adaptations to Periodic Flooding

24.6.1 *Morphological, Physiological and Phenological Adaptations*

Terrestrial and aquatic phases occur under tropical temperature and light conditions that are throughout the entire year optimal for plant growth and development, implying the need for adaptations of trees to long term water-logging and shallow flooding. Trees do not persist in a dormant state, but grow vigorously during most of the year, including the aquatic period. The flooding period of Amazonian floodplains does not correspond to a temperate winter ('physiological winter' *sensu* Gessner 1968) implying reductions of growth and metabolic activity to complete dormancy as observed for trees of temperate forests in the period of unfavorable growth conditions.

Although in Amazonian floodplains the terrestrial phase is the main growth period for tree species, at high water the periods of limited growth last only few weeks, and new leaf flush, flowering, and fruiting occur in most trees while flooded (Parolin et al. 2010c). This requires a number of adaptations which allow growth despite waterlogging or submergence (Fig. 24.3).

Adaptations to flooding in plants are usually considered as either tolerance adaptations or else avoidance mechanisms (Crawford 2003). In the former, metabolic adaptations have been found which allow some plants to endure anaerobic conditions for a length of time sufficient to overcome the period of oxygen deprivation caused by flooding. In the latter, aerenchyma and other structures facilitate aeration of the inundated root. Both these aspects of flooding are by no means mutually exclusive as shown by many Amazonian floodplain tree species.

In some species, the severe physiological stress caused by anoxic conditions in the root zone is indicated by a reduction of the transpiring surfaces via leaf shedding. In other species, the diurnal patterns of crown sap flow (a surrogate for transpiration) are influenced by the size of the stem water store that acts as internal water reservoir during the day and is refilled during the night. Individuals having larger internal water storage capacity, e.g. *Pseudobombax munguba* maintain maximum or near maximum transpiration rates for a longer period of time (Horna et al. 2010). Water limitation does not lead directly to drought damage on leaves but may indirectly

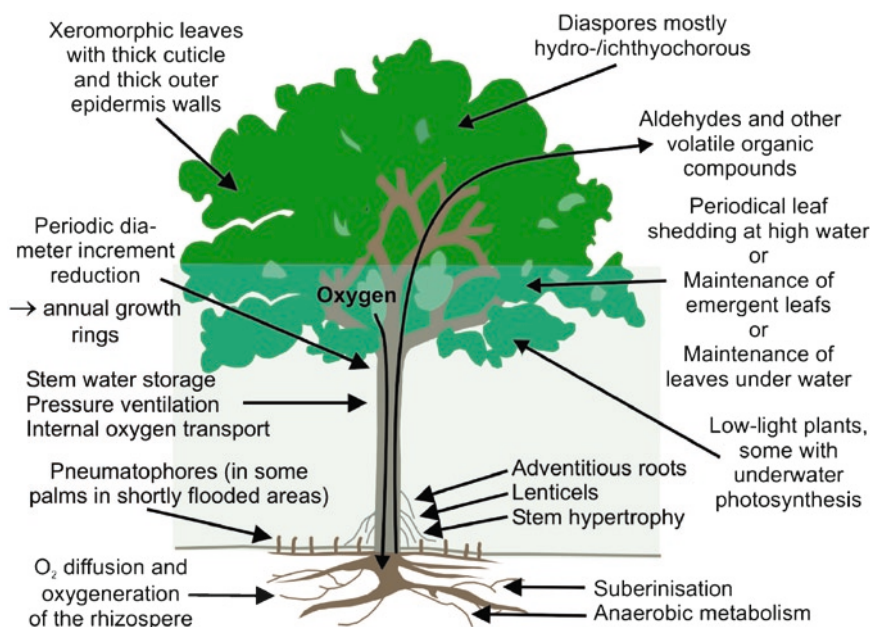


Fig. 24.3 Schematic presentation of morphologic, physiologic and phenologic adaptations of central Amazonian trees to periodic flooding

trigger leaf-shedding e.g. by hormone signals. Reduction in diameter increment of the stem during the flood period (ring formation, Worbes and Fichtler 2010) points to the flood stress for tree growth.

Since trees which have an active sap flow have a need for adequate supplies of carbohydrate also in the flooded period, a set of metabolic adaptations are required for survival and growth despite flooding (Horna et al. 2010). Among these metabolic adaptations we find a large amount of starch for energy supply in the roots of *Eugenia inundata*, a decrease of respiration and a switch to anaerobic pathways as shown for *Astrocaryum jauari* and *Macarobium acaciifolium*.

A primary morphological plant strategy in response to flooding is the development of air spaces in the roots and stems which allow diffusion of oxygen from the aerial portions of the plant into the roots (Jackson and Armstrong 1999). Thus the roots do not have to depend on getting oxygen from the soil. Yet, different trees evolved different strategies to cope with the periodical flooding. Soil inundation usually inhibits root formation and branching, and growth of existing roots and mycorrhizae (Kozłowski 1997). This is not the case in Amazonian floodplains, where tree roots grow below water and mycorrhizae are not affected (Meyer et al. 2010; Haase and Rättsch 2010).

The different permeability of root types, which is determined by their morpho-anatomy and degree of suberization, results in three main strategies described by De Simone et al. (2002b, 2003) and Haase and Rättsch (2010).

- 1 No suberization and strong radial oxygen loss (ROL): Well oxygenated aerenchymatous adventitious roots which are able to build up a several millimeters thick oxygenated layer around the whole roots, suggesting a mechanism of detoxifying reduced phytotoxins by ROL. This is the case in the fast-growing pioneer *Salix martiana*.
- 2 Weak suberization and limited ROL: Deposition of suberin in radial (Casparian bands) and tangential cell walls of the exodermis equips the root with a hydrophobic barrier that contributes to the plant's overall resistance. In this way, exchange between root and rhizosphere is not completely inhibited, enabling the loss of toxic ethanol, but also the entry of reduced phytotoxic compounds into the roots.
- 3 Strong suberization and no ROL: A heavily suberized exodermis starting immediately behind the root tip limits radial oxygen loss (ROL) from the root to the rhizosphere in oxygen-depleted soils and inhibits the entry of toxic substances and infection by microbial pathogens but also inhibits release of ethanol, e.g. in *Tabernaemontana juruana*.

Root aeration, respectively the production of toxic ethanol by alcoholic fermentation in the roots may lead to the emission of considerable amounts of ethanol, acetaldehyde and acetic acid from the canopy of the floodplain forest. Experiments with 2–3 years old tree seedlings of four floodplain tree species under greenhouse conditions showed no emission of these substances under non-flooded conditions (Rottenberger et al. 2008). Flooding of roots resulted in the emission of ethanol and acetaldehyde in all species while emissions of acetic acid occurred only by the

species exhibiting the highest ethanol and acetaldehyde emission rates. All three compounds showed a similar diurnal emission profile, each displaying an emission maximum in the morning, followed by a decline in the evening. This concurrent behaviour supports the conclusion, that ethanol is transported from the roots to the leaves with the transpiration stream and finally partly converted to acetaldehyde and acetic acid by enzymatic processes. Emission rates substantially varied among tree species, with maxima differing by up to two orders of magnitude ($3\text{--}200\text{ nmol m}^{-2}\text{ min}^{-1}$ for ethanol and $5\text{--}500\text{ nmol m}^{-2}\text{ min}^{-1}$ for acetaldehyde). Acetic acid emissions reached $12\text{ nmol m}^{-2}\text{ min}^{-1}$. The observed differences in emission rates between the tree species are explained by root adaptive strategies to tolerate long term flooding. Species which develop morphological root structures allowing for enhanced root aeration produced less ethanol and showed much lower emissions compared to species which lack gas transporting systems, and respond to flooding with substantially enhanced fermentation rates. Considering the large areas covered by floodplain forests, emissions of ethanol, acetaldehyde and acetic acid from the canopy may play a significant role in Amazonian air chemistry at least during flood periods.

In contrast to the manifold adaptations at the root level, astonishingly the morpho-anatomy of leaves (Waldhoff and Parolin 2010) does not show a close relationship between leaf parameters and the periodicity of flooding. The measured variations, e.g. in leaf mass and size, are not understood as adaptations but rather as genetically fixed characteristics of the tree genera which immigrated from the terra firme. For example, the xeromorphic leaf structure found in the floodplain species (Waldhoff and Parolin 2010) is typical for trees of tropical forests in general. Xeromorphy helps to cope with insufficient water supply to the tree crowns during the aquatic phase, and with periods of drought occurring occasionally in the terrestrial phase. Apparently, the leaves which are not shed and maintain their functions despite prolonged submergence do not require different or additional morphological traits. The development of densely packed stacks in the chloroplasts and the low chlorophyll a/b ratio point to high photosynthetic efficiency under low light conditions, enabling the plants to maintain photosynthesis at low levels under water (Waldhoff and Parolin 2010). The same is true for leaf shedding which may not be a strategy against water loss but rather an endogeneously triggered rudiment related to the species' origin. Stem succulent trees of the Malvaceae family (former Bombacaceae) for example originate in semi-arid environments, drought avoidance being enhanced by leaf shedding. This behaviour may have facilitated immigration into the floodplains (Kubitzki 1989a, c), by overcoming first flood stress to water uptake by the fine root system.

A new development in flooding ecology is the unravelling of the molecular regulation of hormonally controlled processes. The expression of an ethylene receptor gene in *Rumex palustris* was highlighted by Blom (1999) and it may be expected that Amazonian floodplain trees exhibit similar genes. When we look at the physiological performance of the trees, it becomes evident that mechanisms which have not been described yet must be acting which enable the plants to survive in this ecosystem.

24.6.2 *Phylogenetic Development of Adaptations*

Flooding stress is a strong driver of adaptive evolution (Jackson and Colmer 2005). The regularity of the recurrence of flooding, i.e. the predictability of the flood pulse (*sensu* Junk et al. 1989), enhances the evolution of specific adaptive traits and may have led to the large variety of species which are able to successfully colonize, establish and dominate the floodplains. Morphological adaptations may be remnants of pre-adaptations from the non-flooded terra firme species where floodplain trees originate from. The degree of flood tolerance may also depend on the time taken to colonize the floodplains. Some species have the potential for the development of adaptive traits – as revealed in waterlogging experiments with seedlings (Haase and Rättsch 2010) – but do not show them in the field in average years. For example, under natural conditions in the floodplains, adventitious roots, lenticels, or stem hypertrophy were observed only in few individuals probably due to the constant change in water level. Although not frequently encountered in the field, their function may be important in years with flooding anomalies.

Recent genetic studies emphasize the continuous adaptation to different habitats as driving force initiating diversification (Ferreira et al. 2010). The genetic separation of individuals of *Himatanthus succuba* in geographically and ecologically continuous environments shows that terra firme vs. floodplains could act as speciation sites. Seedlings growing in the várzea all survived a prolonged period of waterlogging, whereas 30% of the seedlings from the terra firme died when subjected to waterlogging. With complete submergence, in the várzea population 30% of the seedlings had died after 120 days, in the terra firme population after 90 days mortality was 100%.

The várzea forest thus can be regarded as an environment capable of promoting recurrent adaptive changes in plants, which enhances metabolic adjustments and morphoanatomical modifications. The feature which favors the action of natural selection in these environments is the flood pulse. The terra firme acts as a pre-selective environment providing habitats with periodically waterlogged soil conditions. Flooding intensities are longer and higher on the lower levels in the flooding gradient so that the flood pulse causes a species zonation along the flooding gradient. These conditions could promote population isolation and act as barriers to gene flow between individuals of the same species that live in these two ecosystems. In this way, the flood pulse can be seen as driver for speciation as postulated by the Species Colonization Concept (Fig. 24.1; Wittmann et al. 2010).

24.6.3 *Seeds and Seedlings: Chemical Composition, Dispersal and Fate*

High resource allocation to seeds may reflect the need for fast initial seedling growth. Seedlings which are able to protrude the highest possible portion above the

water surface before the next flood period have higher survival chances than seedlings which soon get fully submerged. In the Amazon floodplain, the time before the next flooded period is limited to few months a year and survival rates of the seedlings will be higher if a certain height can be achieved before the onset of flooding. Thus, the need for rapid height growth may have selected for species with larger seeds which enable seedlings to be less dependent on soil nutrients. This however was not found in nutrient-rich várzea, where species growing at high and low elevations did not show any differences in seed mass. Significantly higher seed masses were found only in nutrient-poor blackwater floodplains, on sites with short periods of flooding, i.e. on high levels in the flooding gradient in igapó. In várzea, nutrient reserves are available from the environment and the need to supply the seedling with nutrients from the parental tree is small. This is not the case in igapó, where the environment provides very little nutrients and the seed resources which are particularly important for early growth of seedlings have to be supplied by the parental tree. Only at high levels in the flood gradient fast height growth is an important survival strategy, which on low levels and a water column of many meters is not efficient. Investigating the growth behaviour of seedlings from 19 várzea tree species, Oliveira Wittmann (2007) confirmed this hypothesis showing that some high-várzea species were characterized by height increments of more than 1 m during a period of less than 180 d. Further research on the growth behaviour of floodplain tree species is needed to interpret different growth strategies as adaptation on flooding and/or other environmental factors.

A second explanation for the high energy reserves of seeds might be linked to the close relationship between seeds and fishes. Most Amazonian floodplain fruits eaten by fish have a high fat and protein content, so that the caloric value and delivered energy are high (Waldhoff et al. 1996; Parolin et al. 2010b). The costly allocation of energy reserves to the seeds makes sense in the light of long-distance dispersal, and even more when considering that fish can also transport seeds upriver against the water current. Long-distance dispersal plays an imminent role especially because the biota of Amazonian floodplains is less shaped by in situ speciation and radiation, but more by an equilibrium of immigration and extinction (Wittmann et al. 2010). This stands in contrast to most island and continental biotas and vegetational patterns, where the contrary is normal: the biota are mostly shaped by in situ speciation rather than an equilibrium of immigration and extinction (Price and Elliot-Fisk 2004).

As a first step to establishment, seed dispersal mechanisms play a crucial role, and are frequently linked to the abundant water in form of hydro- and ichthyochory (Parolin et al. 2010b). However, many animals involved in seed dispersal are also seed predators, and the efficiency of dispersal mechanisms has not been measured. Therefore the mere interpretation of the diaspore structure and the potential distribution mechanisms may result in misleading conclusions. Today, many of the tree species of the várzea forests are the most widely distributed in Amazonia, partially because of the persistence of floodplain forests along river systems during very long geological periods (Junk and Piedade 2010) and partly because of the ease of diaspore dispersal by water and fish.

Many floodplain tree species produce diaspores during the aquatic phases (Parolin et al. 2010c; Wittmann et al. 2010). The diaspores may float during variable periods on the water surface or sink to river and lake bottoms. The contact of the diaspores with the river water is controversially discussed in literature. While some authors interpret the contact with the water surface as to be the most important factor breaking seed dormancy, other authors argue that submergence prevents the seeds from oxygen supply that is necessary for respiration and to initiate germination (Oliveira Wittmann et al. 2010). In Amazonian várzea forests, viability of seeds that are in contact with the river water varies between 48 h (*Salix martiana*) to up to 5 months (*Piranhea trifoliata*). Germination experiments indicate that some várzea tree species show faster germination and higher germination rates when subjected to experimental flooding (Oliveira Wittmann et al. 2010). But our knowledge about the different germination strategies is extremely scarce and more germination experiments are necessary.

In contrast to the environmental conditions in Amazonian terra firme where seedling establishment is mainly keyed to the light-demand of tree species (i.e., Bazzaz and Pickett 1980; Denslow 1980; Whitmore 1989), seedling establishment in Amazonian floodplain forests is primarily determined by the flood pulse (Junk et al. 1989). Seedlings establish during the terrestrial phases and often must cope with full and prolonged submersion in the early life stages. Despite hypoxic conditions below water, in black- and whitewater they are deprived of light for many months due to low water transparency and suffer hypoxic or even anoxic conditions in soil and water. However, mortality rates in 459 seedlings of the várzea tree species *Eschweilera ovalifolia* and *Vitex cymosa* that were monitored before and after an aquatic phase in a low-várzea forests near Manaus (mean inundation depth 6.5 m, corresponding to 210 days year⁻¹) amounted to only 2.5% and 33%, respectively (Oliveira Wittmann et al. 2010), values that were surpassed by the establishment of new individuals of the same species during the following terrestrial phase.

Tree seedling establishment and mortality in várzea forests depend on forest succession, which is strongly interrelated to flooding (Wittmann et al. 2010). Most várzea tree species are well-adapted to very small ecological amplitudes and habitats, and forest succession implies that for most várzea species the optimal range of conditions are present only during a restricted period within the successional sere. Many of the trees do not successfully compete when regenerating at the same site as the parent trees. Despite the high impact of flooding, establishment of overall-dispersing early-successional species occurs frequently. Seedling densities in early-successional stages can amount to more than 2,000 individuals m⁻² (Oliveira Wittmann et al. 2010). However, mortality rates in early-successional species amount to at least 99.98% (Wittmann et al. 2010). The proceeding forest succession and decreasing impact of flooding lead to an increased number of tree species with low but more efficient reproduction strategies. Seedling densities in late-successional forests are low, but so are mortality rates.

24.7 Photosynthesis, Primary Production, Biomass and Timber Production

24.7.1 Photosynthesis

Photosynthetic activities of Amazonian floodplain species change in the annual cycle, and the whole physiological apparatus is perfectly well adapted to the regular flood pulse. Under waterlogged conditions, most species show a reduction of mean CO_2 -uptake in aerial leaves ranging from 10% (early successional *Cecropia latiloba*, *Senna reticulata*) to 20–50% (late successional *Nectandra amazonum*, *Crateva benthami*, *Tabebuia barbata*, *Vitex cymosa*) lower CO_2 -uptake than in the terrestrial phase (Parolin et al. 2004b; Parolin et al. 2010a). CO_2 -uptake rises again before the end of the flooded phase and remains high throughout the terrestrial phase (Parolin 2000a). Single measurements – in contrast to average values of the complete aquatic period – show that photosynthetic activity during waterlogging could reach the same or even higher values than in the terrestrial phase in almost all analysed species (Parolin 2000a). Waterlogged adults or seedlings of *Senna reticulata* often showed higher assimilation rates than non-flooded individuals: in a flooding experiment, waterlogged seedlings had an average assimilation rate which was 15 % higher than that of the well-watered control (Parolin 2001c). *Senna reticulata*, flooded by a water column of 4 m with only few leaves appearing above the water surface showed assimilation rates of up to $25 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$, which represent the highest photosynthetic activity measured in waterlogged Amazonian floodplain trees (Parolin 2001c). In several species, the influence of drought appeared to be by far more harmful than that of waterlogging or even submergence in terms of growth, photosynthetic performance and vitality after stress end (Waldhoff et al. 1998). In fact, drought may represent more of an impairment to survival than flooding to the local vegetation (Keel and Prance 1979; Scarano et al. 1994). This gains an increasing importance given the climatic changes which are predicted for the future in the Amazon basin (Malhi et al. 2008). Seedling recruitment and photosynthetic activity may become affected by increasing drought events and this may result in productivity changes and shifts of species composition.

24.7.2 Primary Production, Carbon Stock and Carbon Cycle

The high nutrient stocks in the alluvial soils (Furch 2000) and the periodic nutrient input by floods result in a high productivity of the várzea. A critical nutrient may be nitrogen, however the legume trees, which occur in large species and individual numbers, compensate possible nitrogen deficits by nitrogen fixation, which adds $17\text{--}20 \text{ kg N ha}^{-1} \text{ year}^{-1}$ to the budget (Kern et al. 2010). Várzea forests are among the most productive tropical forest ecosystems worldwide with estimated aboveground net primary productions of $6.6\text{--}15.1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ (Schöngart et al. 2010b). But

carbon stocks and fluxes in aboveground coarse wood biomass (AGWB) differ considerably among floodplain forest types. Young successional stages have low carbon stocks in the AGWB, but high net carbon sequestration rates, while old-growth várzea forests have high C-stocks in the AGWB, but almost no net carbon sequestration. The carbon stock in the AGWB of the entire várzea forest ecosystem, however, is more or less balanced, since the carbon sequestered during the first 50–100 years of primary succession is lost by natural tree mortality and forest destruction due to lateral erosion by the river and channel migration.

The carbon cycle in the AGWB of várzea forests differs considerably in comparison to the non-flooded terra firme forests. Central Amazonian várzea forests have C-storages in the AGWB with up to 120 Mg C ha⁻¹, while terra firme forests stocks about 116.0–195.5 Mg C ha⁻¹ (Chambers et al. 2001). C-sequestration rates in the AGWB of várzea forests vary from 8.5 Mg C ha⁻¹ year⁻¹ in the early successional stages to 2.7 Mg C ha⁻¹ year⁻¹ in old-growth forests. In the terra firme old-growth forests the C-sequestration in the AGWB is about 2.1 Mg C ha⁻¹ year⁻¹. This results in a two to three times lower mean carbon residence time in the várzea (higher C-turnover) when compared to non-flooded terra firme forests, characterizing the high dynamical processes of this ecosystem. But also the interannual short-term C-sequestration in the central Amazonian várzea forests differs from adjacent terra firme forests due to a displacement of two to three months between the growth rhythms of trees in both ecosystems with consequences in their function as short-term climate-induced carbon sinks and sources (Schöngart et al. 2002, this chapter b). The growth rhythms of trees in the terra firme are mainly controlled by the seasonal precipitation, while in the várzea forests these are mainly triggered by the flood-pulse.

The El Niño-Southern Oscillation originating from the equatorial Pacific associates both, the interannual variation in precipitation and flooding patterns in central Amazonia. It causes exceptional droughts during the rainy season in the Amazon leading to climate-induced C-releases from large regions of the terra firme to the atmosphere (Prentice and Lloyd 1998; Foley et al. 2002). During these events, however, parts of the várzea forests can be considered as C-sinks, because the flood-pulse is weakened and the extension of the vegetation period results in higher increment rates and thus higher C-sequestration rates (Schöngart et al. 2004). This duality of biogeochemical sinks and sources in adjacent forest ecosystems is not considered in existing estimates of carbon fluxes based on biogeochemical models, measurements of gas fluxes or accumulation of carbon in vegetation and soils in the Amazon basin. However, data on C-storage and C-sequestration available for floodplain forests still remain underrepresented considering their wide geographic distribution and different forest types as a result of varying climatic, edaphic and hydrologic factors. Especially for the igapó along black-water and clear-water rivers only very few estimates are available (Malhi et al. 2004; Stadler 2007). These studies characterize the igapó forests as ecosystems with C-stocks in the AGWB in the range of várzea forests, but much lower C-sequestration rates and lower C-turnover. Tree-ring studies comparing tree growth of three species occurring in both systems under similar hydrological conditions confirmed the significant lower tree growth in the igapó compared to the várzea (Schöngart et al. 2005; Fonseca Júnior 2007).

Therefore igapó forest ecosystems, especially those along nutrient-poor black-water rivers, should be excluded from forest management activities and permanently protected by the creation of large conservation units (Schöngart 2010).

24.8 Actual Use and Management Options

24.8.1 *Traditional and Modern Management Options of the Várzea*

The várzea has been used and settled by a human population for centuries conducting agriculture, pasture, fishing, hunting, and the extraction of timber and non-timber products as a function of water-level fluctuations (Junk et al. 2010a). Commercial fishing occurs mainly during the low-water period, when fishes are concentrated in the remaining, often isolated water bodies.

Planting of crops is performed at the beginning of the terrestrial phase and the harvest at their end. Logging starts before the water reaches the forests and the timber is skidded and transported during the flooded period. In the Mamirauá Sustainable Development Reserve (MSDR), about 70% of the domestic income of an average household comes from fishery (Schöngart and Queiroz 2010) and consequently the income is high during the terrestrial phase and low during the high water period when economic activities are mainly restricted to timber extraction (Fig. 24.4).

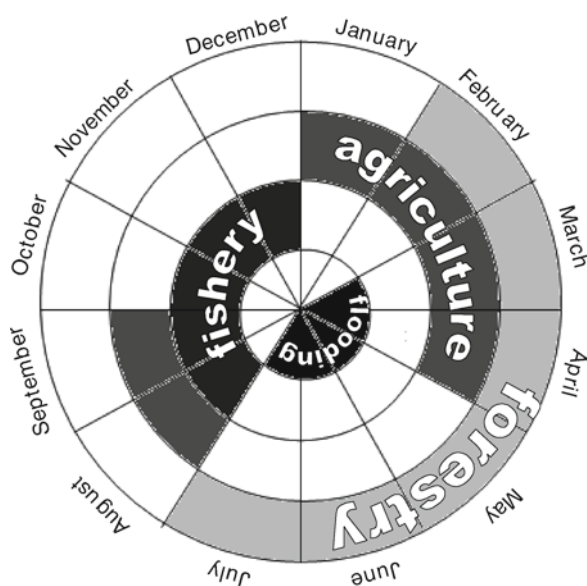


Fig. 24.4 Annual cycle of economic activities of riparian people in the Mamirauá Sustainable Development Reserve related to the seasonal variation of the water level

Management plans involving local communities have been successfully developed, tested and implemented in the MSDR based on a large number of environmental, biological-ecological and socio-economic studies (Queiroz and Peralta 2010). The community-based fishing of the giant pirarucu (*Arapaima gigas*), for instance, resulted in increasing fish populations and increasing incomes for the involved riverine population during the last ten years (Castello 2007).

Modern crop farming, animal ranching, fisheries and their impact on the várzea ecosystem have been studied near Manaus (Junk et al. 2000a). The following table indicates land and labor productivity of the different production systems (Junk et al. 2000b). Data on the land and labor productivity of the different production systems and calculations of timber productivity are presented in Junk et al. (2010a). An environmental impact analysis indicates cattle and water buffalo ranching as most detrimental for the environment because it destroys in large scale the floodplain forest for the establishment of natural and artificial pastures. Land productivity is low but compensated by relatively high labor productivity, resulting from a very low number of herdsmen employed by the ranchers. Negative impact is severe on fishery, habitat diversity and stability, and biodiversity. In contrast, the impact of selective logging is considered low when sustainability is guaranteed by adapted management methods, because it little affects fisheries and other environmental services (Junk et al. 2010a).

24.8.2 Management of Várzea Resources and Water Level Prediction

The timing of flooding and drought dramatically affect the exploitation of the natural várzea resources. The temporal pattern of the water level is more or less predictable. Highest water levels in Central Amazonia occur mostly in the 2nd half of June, while the lowest water levels appear in the 2nd half of October/1st half of November (Irion et al. 1997). However, the height of the minimum and maximum levels varies considerably from one year to the other. Recently developed models to forecast low and high water levels based on tropical Pacific and Atlantic sea surface temperatures (SSTs) (Schöngart and Junk 2007) are powerful instruments to increase the efficiency of planning and executing of the economic activities. In years of low maximum water levels, for instance, the high várzea does not inundate and harvested logs can not be skidded and get rotten causing economical damages for the riverine people and ecological damages on the forest ecosystem. Forecast models, however, allow predicting the maximum flood level already 100 days before its occurrence (Schöngart and Junk 2007) and areas for timber extraction can be selected according to the forecasted water level thus avoiding economic and ecological damages (Fig. 24.5).

Change in precipitation is probably the most critical deterrent in the climate fate of the Amazon. The extreme low water level in many regions of the Amazon basin in the year 2005 raised the question among scientists whether this phenom-

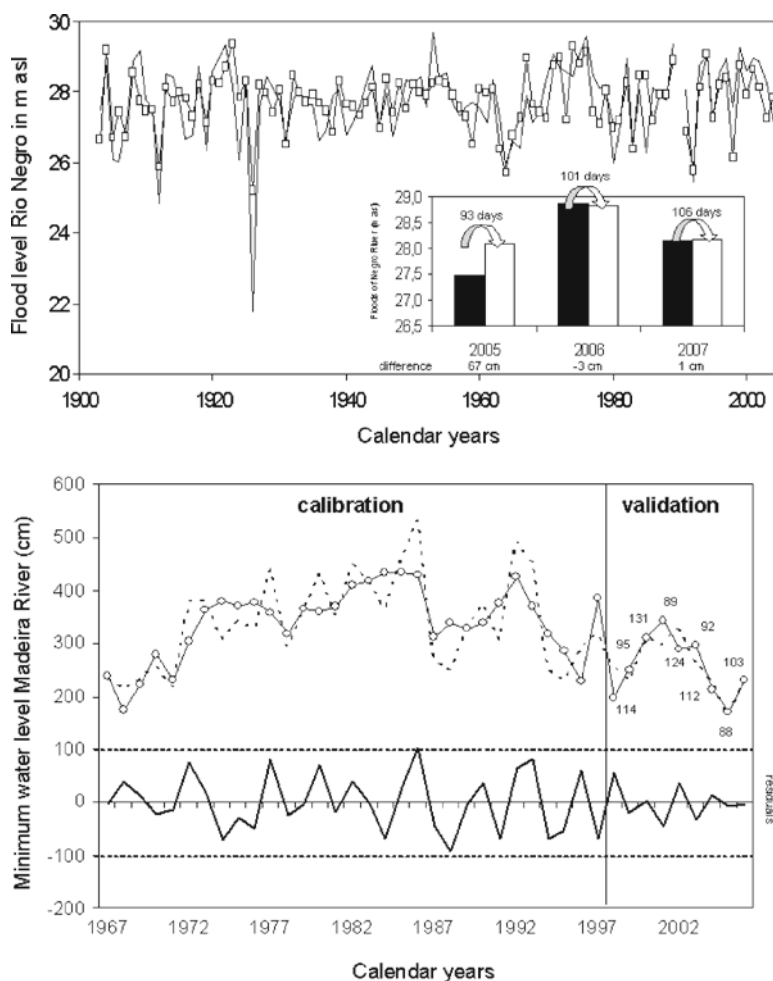


Fig. 24.5 Comparison between the observed (black line) and predicted (dotted line) maximum flood levels of the Negro River (Manaus) for the period 1903–2004 (Schöngart and Junk 2007). The forecasted maximum levels of the Negro River from 2005 to 2007, the difference between forecast (black bars) and observation (white bars) is indicated in the small figure (above). Comparison between observed (black line) and forecasted minimum water levels (dotted line) of the Madeira River at Porto Velho for the period of calibration (1967–1997) and validation (1998–2006). Numbers indicate the period between forecasted and observed minimum water levels in days (below)

enon can be explained by the natural climate variability or if it is a result of the human-induced climate change and/or the consequence of increasing deforestation in the tropics. But due to a missing network of long-term climate records in the Amazon basin this question can hardly be answered. Even the century-long hydrological record at the harbor of Manaus, reflecting mean precipitation conditions in the watersheds of the Negro and Solimões rivers of about 3 Mio. km², does not

indicate if exceptional low water levels or high flooding of the main stem of the Amazon River are the result of man made changes in vegetation cover, and if they still are in the range of their natural climate variability or already a result global climate change (Schöngart and Junk 2007).

24.8.3 *Traditional Use of Timber and Non-Timber Forest Products*

Timber exploitation concentrates on a few species mainly from the high-várzea forests, which stores the most part of timber species, and which only cover approximately 10–15% of the floodplain (Wittmann and Oliveira Wittmann 2010). Easy access combined with the low cost of timber harvesting, processing, and transport led to the overexploitation of many floodplain trees soon after the intense immigrations associated with the rubber boom (1850–1920) (Santos 1980). Although the area covered by floodplain forests is smaller than the accounted for by Amazonian terra firme, about 70–75% of the wood exploited in Amazonia before the mid-1970s originated from the floodplains, because most of Amazonian settlements are located along or close to Amazonian white-water rivers. In the Brazilian Amazon, wood production in floodplains contributes US\$ 120 million to the Amazonian gross product and currently directly generates about 30,000 jobs (Bentes-Gama et al. 2002). Most timber species are locally used for house construction, carpentry, furniture, and boat, houseboat, and canoe construction (Wittmann and Oliveira Wittmann 2010).

The use of floodplain forests has been unsustainable and often illegal, over most decades of the twentieth century. Tree species such as *Ceiba pentandra*, *Virola not surinamensis*, *Cedrela odorata*, *Calophyllum brasiliense* and others have been intensively harvested for few decades without any information on tree ages, growth rates, germination and seedling establishment and growth. Due to the decline of the species population these tree species almost disappeared from the local and regional markets and have been substituted by tree species with similar wood characteristics such as *Hura crepitans*, *Ocotea cymbarum*, *Calycophyllum spruceanum* and *Maquira coriacea*. But also for these species information on tree growth and regeneration does rarely exist. If intensive harvest on these species continues they may have similar destinies as the earlier generation of timber species in the várzea (Schöngart and Queiroz 2010).

An increased timber extraction from the várzea forests and the competition between forest management and other land-use options (agriculture, pasture, settlement) requires strategies and concepts for the long-term conservation of the floodplain forests. In this context, a large number of participatory community-based forest management, and forest management on small scales (private properties < 500 ha), have been established in recent years in the MSDR and within the frame of large development programs such as PPG7–Projects Pro–Manejo and Pro–Várzea. In the Amazonas state > 600 management plans for small-scale private properties and

community-based forest managements have been implemented, mainly in várzea floodplains along the Solimões, Amazonas, Juruá, and Madeira rivers (Schöngart and Queiroz 2010). Most of these projects promote selection harvest combined with reduced impact logging as sustainable forest management. Due to the legalization of a controlled timber extraction wood prices increased up to ten times within a decade in the central Amazonian region. The traditional community-based forest management, established in 2000, experienced an over 200% increase of wood prices due to the legalization of the timber extraction and political structuring of the local people by creating local associations. In the MSDR, it improved significantly the financial status of the involved associations especially during the flooded period when the income of an average household is very low (Schöngart and Queiroz 2010). But these technical and logistical improvements for timber extraction are not sufficient to provide a sustainable management of the timber resources, as shown later.

Besides timber, the economic potential of non-timber forest products (NTFP) in Amazonian floodplain forests is exceptionally high, because nearly all stems present in forest inventories can be useful to the inhabitants (Phillips et al. 1994). In addition, their role as a buffer in times of food shortage makes NTFP a critical component in the food security of rural populations (Lipper 2000). While in the western Amazonian floodplains up to 87% of all tree species present in forest inventories are useful to the floodplain inhabitants, approximately 53% of all tree species provide NTFP in central Amazonian floodplains (Wittmann and Oliveira-Wittmann 2010). Many NTFP are of subsistence or indirect values to the inhabitants, and their value thus difficult to measure. Phytomedical products and edible fruits are among the most important use categories of NTFP in Amazonian floodplains, but a variety of other uses can be of huge local or even regional importance, such as fruits used as fish bait, fruits and wood for handicrafts, palm-heart extraction, latex and resins for fishing and hunting poisons, fibres for tying and braiding, oil, fuel, dyes, containers, or construction material in general (Wittmann and Oliveira-Wittmann 2010).

Ethnobotanical inventories about the uses of NTFP in floodplains are practically absent within the Brazilian part of the Amazon basin, and their economical importance including possible variations between the Amazonian flooded ecosystems and along the river system remains widely unknown. Most information about the use of forest resources originates from the Amerindian population, which may differ substantially from the use of colonialists. While the Net Present Value (NPV) of timber depends on the regional, national, and international timber markets, and thus can easily be quantified, much remains to be learned about the economic value of NTFP. The value of many NTFP to the local inhabitants may be indirect and thus difficult to measure. Additionally, the NPV of phytomedical and phytocosmetical products is mostly unknown and/or undervalued by extractors, thus depriving inhabitants of a fair economic return. However, an increasing effort in ethnobotanical inventories could not only be important for the improvement of communally sustainable forest management plans, but it also would provide essential information for authorities about how to supply the rural population during periods with catastrophically low or high water levels.

24.8.4 *Growth-Oriented Logging (GOL), a New Forest Management Concept for Timber Production*

The long-term success of forest management in the várzea and other multi-species forest ecosystems requires information on species-specific and site-specific growth rates to determine sustainable harvesting volumes and cutting cycles. However, the current Brazilian forest legislation considers only one cutting cycle and one minimum logging diameter (MLD) to manage a high variety of timber species of different forest types. In the várzea, there is the risk of overexploitation of slow-growing timber species, while the fast-growing timber species with low wood densities are not efficiently used (Schöngart 2010). The new concept “Growth-Oriented Logging – GOL” developed by Schöngart (2010), has been created as an aid to improve the forest management in the MSDR and central Amazonian várzea. GOL is based on species-specific and site-specific management criteria, such as MLDs and felling cycles derived from growth models based on tree-ring analysis, which is unique for tropical silviculture (Fig. 24.6). Due to the occurrence of annual rings in tree species of many tropical regions (Worbes and Fichtler 2010), such growth models and concepts can be established also for other timber species and forest types.

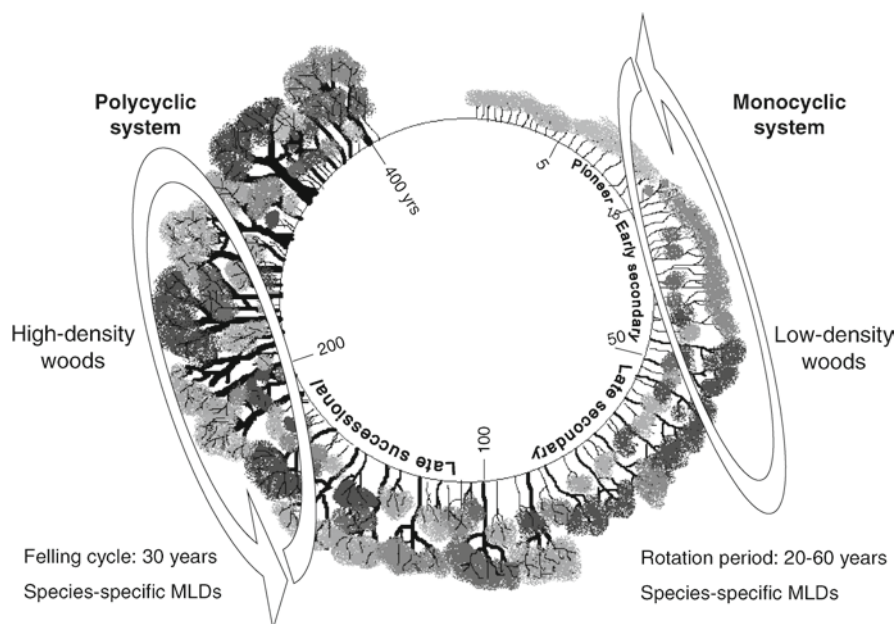


Fig. 24.6 GOL – Growth Oriented Logging: a silvicultural concept based on growth models derived from tree-ring analysis. The sustainable use of fast growing low-density woods in early and late secondary stages is achieved by monocyclic systems and that of slow growing high-density woods in late successional stages by polycyclic, selective systems (Schöngart 2010)

However, felling cycles or rotation periods only guarantee a sustainable use of the timber resources, if the harvested species continue to recruit. Little information is available on germination, growth, and establishment of seedlings and saplings as well as their relationship to external abiotic (flooding, light conditions, water and nutrient supply) and biotic factors (seed banks, inter-specific and intra-specific competition, herbivory) (Piedade et al. 2010). Further studies should therefore focus on the germination, growth, and mortality rates of seedlings of timber species and their relationship to environmental factors. Cost-benefit analyses are necessary to evaluate silvicultural improvements, such as enrichment plantings and thinning to regulate recruitment and competition as well as removing of branches to increase stem quality. Together with data on tree species distribution patterns in dependence of abiotic variables (i.e., inundation, soil characteristics, solar radiation at time of plant establishment, (Wittmann et al. 2010), these data serve for successful reforestation on degraded and deforested sites under optimal conditions, thus lowering the risks of failure.

24.9 Threats and Possible Impacts of Land-Use and Climate Change on Central Amazonian Floodplain Forests

Scenarios of Soares-Filho et al. (2006) indicate increasing deforestation in the Amazon basin driven by the expansion of soybean, sugarcane, cattle industries and major infrastructure programs such as paving and construction of roads, hydroelectric dams, ports, pipelines and waterways. Removal of the forest cover in the catchment area of the large rivers, such as the Madeira and Tocantins Rivers probably leads to earlier and more pronounced discharges due to the higher surface water runoff, as Costa et al. (2003) showed it for the Tocantins River basin in Brazil with a 25% increase in river discharge coincident with expanding agriculture in the catchment area but no major change in precipitation. Between 17 Pg C and 33 Pg C will be released by land use changes in the Amazon basin to the atmosphere until 2050 depending if recent deforestation trends will continue or if the Brazilian environmental legislation will restrict and decline deforestation across the Amazon basin (Soares-Filho et al. 2006). Despite the C-emissions, the release of NO_x , aerosols and black carbon particle to the atmosphere by biomass burning has significant impacts of the oxidation processes, the atmospheric composition and the formation of droplets (Andreae et al. 2004; Oliveira et al. 2007) with serious effects on water balance, formation and lifetime of clouds as well as local and regional precipitation patterns and hydrological cycles. Severe droughts provoked by increased SST anomalies in the tropical Atlantic and Pacific (El Niño) cause climate-induced CO_2 -releases on large areas of the intact Amazonian terra firme (Prentice and Lloyd 1998; Tian et al. 1998; Foley et al. 2002) and especially in regions experiencing forest fragmentation with increased vulnerability to large-scale fires (Nepstad et al. 1999; Laurance and Williamson 2001; Cochrane 2003). Especially for these areas new climate scenarios predict an increased drought probability for the future (Malhi

et al. 2008). These processes increase the release of huge amounts of CO₂ and other greenhouse gases, which feed back and accelerate climate changes (IPCC 2007).

Under this aspect the construction of hydroelectric dams and an industrial waterway as it is planned in for instance for the Madeira River by the Brazilian government within large infrastructure programs (Brazilian Growth Acceleration Program – PAC, Initiative for the Integration of Regional Infrastructure in South America – IIRSA) is very problematic. The establishment of several hydroelectric dams in the upper Paraná River affected its floodplains only within two decades characterized by a significantly declined amplitude of the monomodal flood-pulse leading to a decrease of its seasonal dynamic, loss of sediments retained by the dams causing a decreased connectivity and oligotrophication as well as an increased transparency of the water (Agostinho et al. 2007). These dramatic changes have severe impacts of the functioning of the floodplain ecosystem and its biodiversity favoring the invasion of alien species and causing extinction of other species.

Such experiences can be transferred to the floodplains of the Amazonian rivers where human populations depend on their natural resources to carry out agriculture, animal ranching, fishing and hunting, as well as the extraction of timber and non-timber products in relation to the flood-pulse. Due to the construction of hydroelectric dams nutrient-rich sediments will be retained in the artificial basins also favoring the accumulation of toxic materials like mercury due to the gold mining activities (Padovani et al. 1995). The increase of the water surface area in the artificial basins leads to extended water evaporation and the dams hinder the migration of many commercially important fish species which must reach the catchments for their reproductive cycle (Junk et al. 1997). These negative ecological and socio-economical impacts get more severe in the background of possible lower future water discharges in the large watershed caused by increasing SSTs in the tropical Northern Atlantic and tropical Pacific.

Global climate change models are not yet sufficiently precise to make predictions for the Amazon region for the next century (IPCC 2007; Marengo 2006). There is general agreement that the coastal areas will become affected by a sea-level rise of 20–40 cm. This will lead to a shift of the mangroves further inland, when suitable areas are available, and also affect the floodplains at the lower course of the Amazon river. A reduced river slope will lead to increased sediment deposition in the lower Amazon River valley. However, floodplain forests are dynamic systems and species composition and distribution will adapt to changing sediment deposition and flood stress. After the last glacial maximum, the sea-level raised about 100m in 10,000 years corresponding to a mean increase of 1m per century. Even higher rates of 1.6m per century were found for the last interglacial period (Rohling et al. 2008).

The temperature increase in the central Amazonian lowlands may reach about 4–6°C (IPCC 2007; Malhi et al. 2008). Its impact on the floodplain forest is hard to be evaluated and will become detectable only after many decades, because the reactions of the many tree species to increased temperatures are not sufficiently understood. The Hadley Center climate model coupled to a dynamic vegetation and carbon cycle model indicates during the next few decades a dramatic decrease in carbon stored in central Amazonian soils and vegetation leading from rain forest

cover to a savannah vegetation. We consider such predictions as unrealistic because of the precarious data base. They are also politically dangerous, because they counteract all efforts to protect the rain forest, and may even be used to favor deforestation and soy bean and sugar cane plantations.

Temperature increase may have strong impacts in the high Andes and will lead to accelerated melting of glaciers (IPCC 2007), affecting the discharge pattern of the upper Amazon River and its large tributaries with Andean headwaters. In Central Amazonia these effects will probably be in part compensated by the impact of the different discharge curves of the large tributaries. Until today, no changes in the hydrology of the Amazon River can be detected. Extreme floods related to La Niña episodes such as in the years 1971/72, 1974/76, and 1999 or droughts associated with increased SSTs in the tropical North Atlantic as observed in 2005, respectively, are in the natural range of pluriannual hydrological cycles as shown by a 200 years proxy, based on a tree ring analyses, calibrated for the last 100 years by the hydrological data of the Manaus Harbour Authority (Schöngart et al. 2004; Fig. 24.7).

The predictions about precipitation changes are not yet clear, but a decrease of precipitation in the southern and northern Cerrado belts is probable. Precipitation amounts in the forested parts of Amazonia may continue at the same level but differences between dry and rainy season may increase, increasing the drought stress for the trees during the dry season. Global climate simulation models indicate increasing SSTs in the tropical ocean sectors for the forthcoming decades. This may cause more frequent lower maximum floods related to positive SST in the tropical Pacific (Schöngart and Junk 2007) and probably more frequent and severe droughts in the Amazonian floodplains associated with increased SSTs in the tropical North Atlantic. This points to water availability as the strongest stress factor in Amazonia.

Studies of Nepstad et al. (2001) show that already today, large parts of the terra firme rainforest in eastern Amazonia are vulnerable to fire during strong El Niño periods. Abundant charcoal in terra firme, caatinga and igapó soils near San Carlos de Rio Negro suggest that fire has been in the mid- to late-Holocene a disturbance factor (Sanford Jr. et al. 1985). Our observations in the igapós of the tributaries of the middle Negro River show that these forests are very vulnerable to fire at low water, too. They grow on sandy soils with a low water retention capacity, and have a superficial root system, to avoid anoxic conditions during the flood period. These forests suffer flood stress during flood periods and a heavy edaphic drought stress during strong El Niño periods, which makes them vulnerable to wild fires, as shown by several burned areas delineated on one side by the river channel and on the other by intact upland forest. In the 1920s, the bishop of Barcelos at the middle Negro River reported large fires in the area. Such occurrences are reported for the severe drought during 1925–1927 associated with the strong El Niño phenomenon of 1925/26 (Schöngart et al. 2004) when a full-year drought occurred in the Rio Negro catchment area, with many forest fires lasting for over a month and extremely low river-water levels that impeded river travel (Sternberg 1987). This event is well documented in a report by the Salesian bishop to the Vatican (Sombroek 2001) and

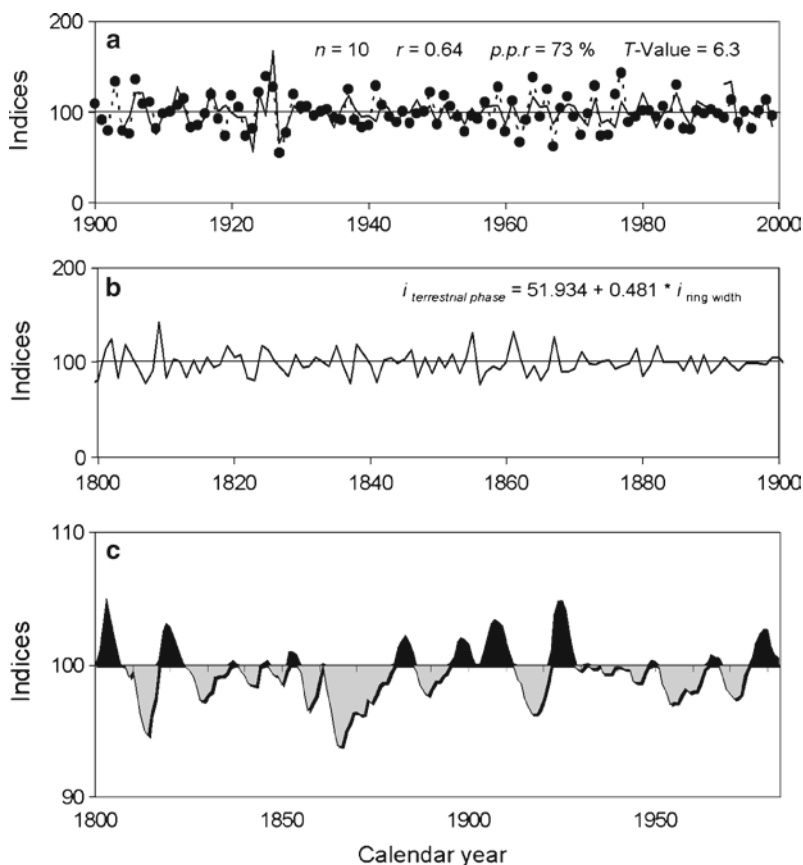


Fig. 24.7 Indexed ring-width chronology *Piranhea trifoliata* (dotted curve) and deseasonalized time series of the duration of the non-flooded period (black curve) derived from the daily recorded water-level at the port of Manaus. The correlation between the two curves is significant ($p.p.r$ is the percentage of parallel run between the two curves). Based on a linear regression model the flood patterns were reconstructed for the nineteenth century (Schöngart et al. 2004)

also by other historical documents for the Caroni River, a tributary of the Orinoco in the Venezuela (Williams et al. 2005).

24.10 Conclusions

After a period of taxonomic studies at the beginning of the twentieth century, Amazonian floodplain forests were let at the sideline of research despite its large economic importance for timber supply in the region. Only in the last decades researchers in Iquitos and Manaus started intensive studies on ecophysiology, primary production, biodiversity and sustainable management. With more than 1,000

confirmed species these studies substantiate the high species diversity. They also show that the várzea forests can be sub-divided in different types and successional stages, which are related to the position of the forest on the flooding gradient. Igapós require additional studies for general statements on species and community diversity. A large number of morphological, anatomical, physiological and phenological adaptations are combined by the trees of várzea and igapó in different strategies to cope with flooding. This supports the postulation of the flood pulse concept (Junk et al. 1989) that indicates hydrology as the major driver in river-floodplain systems. However, phenological behavior often does not fit to the flood pulse periodicity and points to other drivers, e.g. evolutionary traits related to species origin in dryland habitats.

The large number of highly adapted tree species is the result of the existence of large river floodplains and wetlands in South America throughout long geologic time periods without major extinction periods. Strong hydrodynamics led to high habitat diversity and habitat dynamics favoring the co-existence of many species (Intermediate Disturbance Hypothesis, Connell 1978). But it is also the result of the permanent trickling-in of species from the highly diverse upland forest, first to the higher parts of the floodplain and later from there to the deeply flooded lower parts (Species Colonization Concept, Wittmann et al. 2010). Lateral and longitudinal genetic exchange plays an essential role in the development and maintenance of species diversity in the Amazon river floodplain. This holds true also for other species groups, such as fishes, birds, mammals and invertebrates, which live in the floodplain forests and depend on them. Additional genetic studies are required to clarify origin and relationship of the species and better explain speciation processes.

The fertile alluvial soils and the periodic flooding of white-water river floodplains provide the nutrient basis for high productivity despite intensive flood stress, which surpasses the productivity of central Amazonian upland forests by a factor 1.5 to 2 and that of the nutrient-poor igapó by a factor 2 to 2.5. Igapós grow on nutrient-poor soils and have no potential for sustainable timber production, but várzeas belong to the very few areas in central Amazonia, which can be used without risk of nutrient depletion. Growth Oriented Logging (GOL) (Schöngart 2010), provides the conceptional basis for sustainable forest culture with fast growing softwood species in areas covered by early successional stages and selected timber extraction of slow-growing hardwood species in advanced successional stages, without losing diversity, when substitution of the logged specimen is guaranteed by natural rejuvenation or plantation of saplings.

This concept has to be tested in praxis urgently, because the studies show increasing forest degradation by unsustainable logging methods and large scale forest destruction by cattle ranching (Junk et al. 2000b). Exploitation of floodplain forests spread from the urban centers to remote areas even along the lower courses of the large tributaries. Today, most forests along the main stem of the lower Amazon River are heavily degraded or substituted by grassland. Large areas are covered by a species poor secondary forest that grows on abandoned jute plantations, and former pastures. Forests are under permanent pressure by cattle and water buffaloes which negatively affect natural regrowth by trampling and feeding

on fruits and saplings. Crop plantations little affect total forest area because they occupy only relatively small areas on the highest levees, mainly near urban centers which provide a market for the products.

Balancing the predicted impacts of global climate change and the impact of other human activities on Central Amazonian floodplain forests and their biodiversity we can state that serious risks arise, if sustainable management practices are not introduced in environmental policy in the next future and if its implementation is not seriously controlled. Floodplain forests on sandy soils at some tributaries of the Negro River and on shallowly flooded interfluvial wetlands may suffer increased fire stress during El Niño periods and periods of extreme low water levels. Vörösmarty et al. (2000) state that rising water demands will greatly outweigh greenhouse warming in defining the state of global water systems to 2025. We state that unsustainable use will greatly outweigh greenhouse warming in defining the state of central Amazonian floodplain forests to the end of the twenty-first century.